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CONSERVATISM AND VARIABILITY IN THE SEEDLING OF DICOTYLEDONS

EDMUND W. SINNOTT

INTRODUCTION

Ever since the statement of the law of recapitulation by the zoologists attempts have been made to extend it to the plant kingdom and to discover, in the seedling, traces of characters which have been lost elsewhere in the plant and which from their constancy might be used as guides to relationship. External characters, particularly "juvenile" foliage, were at first chiefly studied, but more attention has latterly been paid to internal structure. Jeffrey and his students have investigated the secondary wood of young plants for evidences of conservatism. It is the structure of the actual seedling, however, and its still dominant primary tissues, which has engaged the attention of most students of the subject, foremost among whom are members of the English school of anatomists.

Although numerous instances have been found by these observers where seedling structure is useful for classification, within narrow limits, it must be admitted that the high degree of variability recorded in "type of symmetry," number of protoxylem clusters, number and position of primary bundles, level of transition from root structure to stem structure, and so on, have served in the minds of many to cast doubt on the conservatism of this portion of the plant and have discouraged those who attempt to promulgate the law of recapitulation for the vegetable kingdom. The opinion of the probably majority of workers is expressed by Hill and de Fraine in the following quotation (1, p. 264): "For these reasons we see no necessity for preserving seedling anatomy from the fate already meted out to other structural features, *e. g.*, secondary thickening, which were at one time considered as indicators of phylogeny, a conclusion arrived at, either entirely or in part, by others who have paid attention to the facts of seedling anatomy."

These investigators have in general confined themselves to one or a few families and have studied the relative variability of the

seedling and the mature portions of the plant, looking to the former to provide clues for specific or generic relationship. The present paper records an examination of seedling structure over a wide range of families and orders in the dicotyledons, with a view to determining, on the basis of this comparative study, whether the anatomy of the seedling is variable everywhere, or whether it exhibits any characters which are sufficiently constant to be of value in marking out broad lines of relationship.

The seedlings of over 250 species belonging to 86 families were examined. External characters were observed and recorded and internal structure was studied by means of serial sections.

OBSERVATIONS

The observations of others as to the high degree of variability of certain characters, particularly the number of protoxylem clusters and the level of transition, were confirmed and their uselessness for classification emphasized. Another line of inquiry, however, was

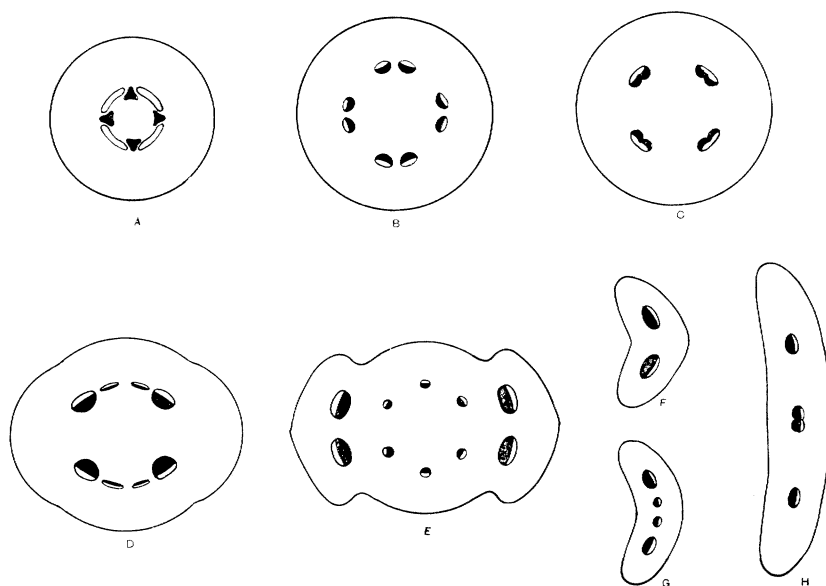


FIG. 1. *Thespesia populnea* (Malvaceae). Serial sections from root to cotyledon. *a*, root; *b-d*, hypocotyl; *e*, node (bundles of epicotyl in central ring); *f-g*, petiole of cotyledon; *h*, base of cotyledonary blade. (Xylem black, phloem white.)

suggested by the fact that in the mature plant the topography of the node, with the number and arrangement of leaf traces and gaps, has been shown (2) to be very constant throughout wide groups. To determine whether or not the characters of the cotyledonary node

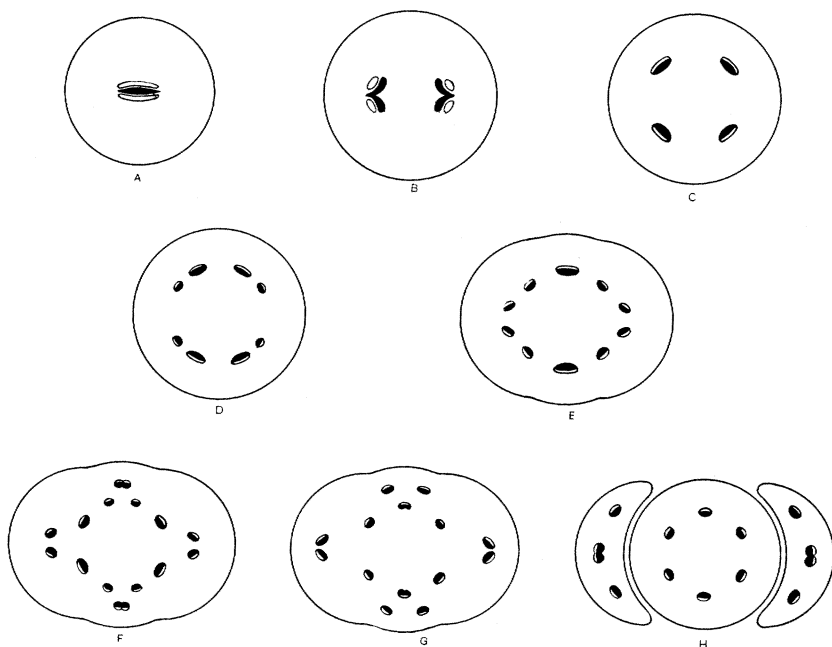


FIG. 2. *Momordica Balsamina* (Cucurbitaceae). Serial sections from root to cotyledon. *a*, root; *b-d*, hypocotyl; *e-g*, node (showing relation of cotyledonary bundles to those of epicotyl); *h*, epicotyl and cotyledons. (Xylem black, phloem white.)

are also slow to change, careful attention was given not only to the vascular supply of the seedling proper, consisting of the cotyledonary traces and their extensions into the hypocotyl, but to the relation between these first strands and those which arise later and form the vascular system of the epicotyl and subsequently the stem of the young plant. It was found that this relationship between the hypocotyledonary and the epicotyledonary systems, a feature hitherto neglected, provides some of the most constant structural characters of the seedling.

By far the most common condition at the cotyledonary node is that shown in figures 1 and 2 and in figure 4, *b*, *c*, and *d*, where the bundles of the epicotyl arise entirely in the intercotyledonary plane and the traces of each cotyledon make but a single gap in the vascular ring. This corresponds to the unilacunar nodal type in the mature

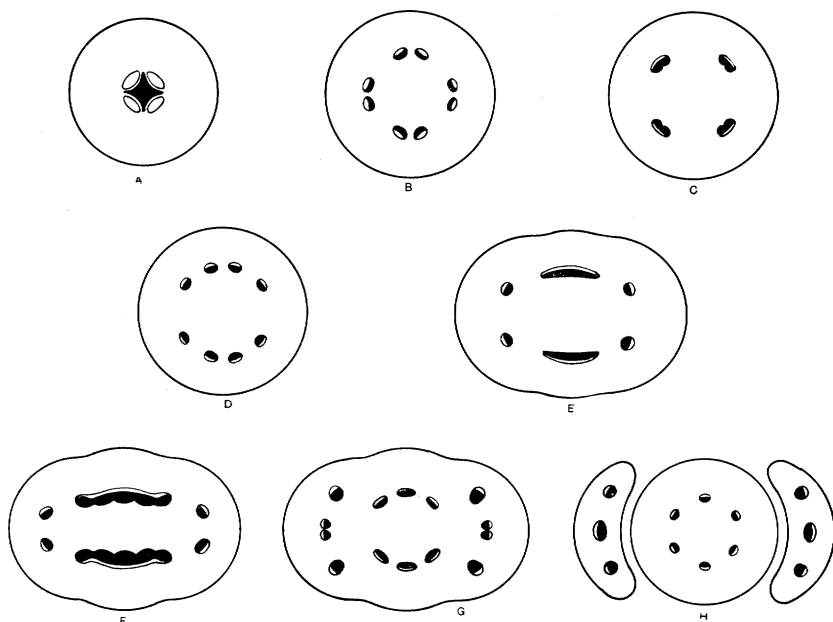


FIG. 3. *Echinops sphaerocephalus* (Compositae). Serial sections from root to cotyledon. *a*, root; *b-e*, hypocotyl; *f-g*, node (showing trilacunar insertion of cotyledonary traces); *h*, epicotyl and cotyledons. (Xylem black, phloem white.)

stem. A number of families, however, show a more complex condition, the epicotyledonary bundles arising between the individual strands of a cotyledonary trace. In figures 3 and 4, *e*, the trace has four strands and the epicotyledonary bundles arise between each lateral and its adjacent central bundle. The vascular supply of each cotyledon thus causes three gaps in the ring (in this case two lateral traces arise from the same gap) and thus corresponds to the trilacunar condition of the mature stem. Several variations on this type were observed. In some cases, bundles of the epicotyl appear at the inter-

cotyledonary poles, separating the adjacent laterals. Sometimes, as in *Ricinus*, epicotyledonary bundles may also appear between the two central strands of the trace, thus causing each trace to leave four gaps in the vascular ring. Sometimes, as in certain of the *Euphorbiaceae*, *Aceraceae* and *Proteaceae* (Fig. 4, *f*), the cotyledonary trace

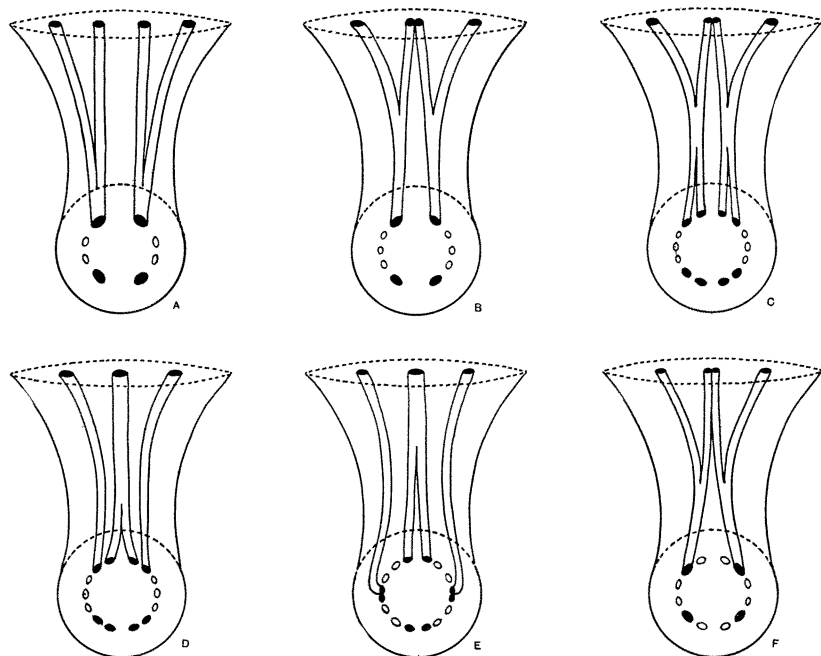


FIG. 4. Diagrams showing cross-sections of node, course of bundles in base of one cotyledon, and section of cotyledon, in six seedling types. *a*, *Ephedra dioica*, gymnospermous type, unilacunar, two trace bundles, no midrib; *b*, *Thespesia populnea*, unilacunar, two trace bundles, giving rise to three-veined condition; *c*, *Lavatera arborea*, unilacunar, four trace bundles fusing into two and then producing three-veined cotyledon; *d*, *Momordica Balsamina*, unilacunar, four trace bundles forming three-veined condition directly; *e*, *Echinops sphaerocephalus*, trilacunar, four trace bundles, forming three-veined cotyledon; *f*, *Grevillea robusta*, bilacunar, two trace bundles, forming three-veined cotyledon. (Leaf traces black in section, epicotyl bundles white.)

may consist of only two strands, but these may be separated by epicotyledonary bundles, a bilacunar node thus being produced. In all these cases the essential fact is that the node is multilacunar, the

vascular tissue of the epicotyl arising somewhere between separate strands of the same trace. This condition, it should be noted, is not simply that of "independent laterals," which may occur in either of the main forms we have described.

These two types of cotyledonary node are very constant through large groups. The unilacunar is much the more common and is invariably present (as far as the writer has observed) in 73 out of the 86 families examined. The multilacunar type was found in the Aceraceae, Berberidaceae, Compositae, Euphorbiaceae, Hippocastanaceae, Magnoliaceae, Melianthaceae, Plumbaginaceae, Polygonaceae, Proteaceae, Sapindaceae, Sapotaceae and Umbelliferae. In the Berberidaceae (*Berberis*) the two lateral strands of the trace are very small and are frequently absent, giving a unilacunar condition. In the Magnoliaceae several genera are unilacunar, as is *Securineca* in the Euphorbiaceae. All the other genera and species of these and the other families named were invariably found to be multilacunar, of one type or another. In the Aceraceae, Sapotaceae and portions of other families there are two gaps at the node; in the others, prevailingly three.

Since the size of the seedling has been shown by Hill and de Fraine (1) to affect the number of protoxylem clusters in the root and hypocotyl and the number of strands in the cotyledonary trace (the larger the seedling, the greater the number) it might also be expected to affect the topography of the node. In very tiny seedlings it may do so, but in no case observed was this found to be true. Some very small seedlings were studied in the multilacunar families, particularly in the Compositae and Umbelliferae, but these were always multilacunar. Many of the largest seedlings, on the other hand (notably the Leguminosae as a whole), are unilacunar.

There is an evident relation between the structure of the node in the main stem and that in the seedling. All families in which the seedling shows a multilacunar condition possess this type in the mature stem also, except in the case of the Sapotaceae. In the 73 families where the cotyledonary node is unilacunar, however, the connection is less definite, for 34, or 47 percent, have a prevailingly unilacunar node in the mature plant; 39, or 53 percent, being multilacunar.

These facts indicate that in the topography of the cotyledonary node we have a character which is much more constant than many of

the anatomical features of the seedling, and that it may be used to distinguish large groups of plants. Of course the number of species studied is far too small to give an accurate idea of what the conditions are throughout the various families, but in those where the largest number of species has been recorded, nodal uniformity is very evident. In several cases both main types are found in the same family. The Ranunculaceae are prevailingly unilacunar, but certain species of *Clematis* seem from their description by Miss Thomas (5, p. 706) to have several gaps. We have recorded a similar situation in *Berberis*, the Magnoliaceae and the Euphorbiaceae. It seems very likely that in many of these less specialized families the seedling node may not be completely uniform. As to its general conservatism throughout the dicotyledons, however, there can be little doubt.

A comparative study of the seedling node will evidently give us much valuable information as to relationships. The multilacunar condition seems to be quite absent in many of the great orders, even in those where the node of the mature stem has several gaps. In others it is invariably present in all species so far examined. In still others, notably the large and heterogeneous orders Geraniales and Sapindales, it characterizes certain families or groups of families but is absent from the rest, thus providing a clue as to relationships within the order. In the Sapindales, for example, the Aceraceae, Hippocastanaceae and Sapindaceae, grouped together by Engler as the sub-order Sapindineae; and the Melianthaceae, comprising the sub-order Melianthineae, are multilacunar. All the rest of the families examined in this order, however, are unilacunar.

As to what has been the evolutionary history of the seedling node we cannot be sure. Evidence has elsewhere been presented (2) that for the mature stem the trilacunar node was the primitive one among Angiosperms. The fact that this is present in the seedling node of only a few families, however, and that these are for the most part by no means primitive in their other characters, suggests that the unilacunar condition of the seedling is a persistence of an ancient gymnospermous condition and that the multilacunar type made its appearance in the node of the foliage leaf and has worked down from thence into the seedling. On the contrary, it may be argued from those cases where the lateral traces in the multilacunar condition are very small, that they are here dying out; and that the unilacunar type has arisen by the complete loss of lateral traces which originally were always present.

A second feature of the structure of the seedling which is constant throughout large groups is the venation of the cotyledon. In the great majority of the families this is palmate and three-veined (3, Plate III), a condition which we have reason to believe is primitive for the Angiosperms. In a few cases, however, it seems to be constantly pinnate, with a strong midrib. This is characteristic, so far as the writer's observations have gone, of the Amaranthaceae, Anacardiaceae, Boraginaceae, Capparidaceae, Celastraceae, Ebenaceae, Moraceae, Myoporaceae, Nyssaceae, Periplocaceae, Pittosporaceae, Polemoniaceae, Rutaceae, Simarubaceae, Solanaceae, and of portions of other families. In all these cases the cotyledonary node is unilacunar, so that there is in the seedling a similar relation between nodal topography and leaf venation which has been found to occur in the mature plant (3).

The most constant and invariable character of the seedling, however, is the double nature of the cotyledonary trace, a fact emphasized by the work of Miss Thomas (4). In the ferns and gymnosperms the trace of the mature leaf, where it leaves the vascular ring, is at least primitively either a double bundle or an arc with an even number of bundles. A radical change brought about at the origin of the Angiosperms was the conversion of this double bundle into a single one or into an arc with an odd number of strands. This change is made evident externally by the development of the strong midrib so characteristic of the leaf of Dicotyledons. In the seedling of the Dicotyledons, however, we find the original condition persisting. The venation of the cotyledon, to be sure, is angiospermous, with a midrib and lateral veins, which distinguish it from the cotyledons of the gymnosperms.¹ At the cotyledonary node, however, the ancient double trace still persists unchanged. *In its essential topography the node of the seedling is the same throughout all seed plants.* In figure 4, *a*, is shown the node of Ephedra, presenting the typical gymnospermous condition, and in the other figures are some of the types found among dicotyledons. There may simply be two traces to each cotyledon or there may be two pairs of traces. In the trilacunar type it will be noted that an even number of bundles is given off, due to the fact that the central gap provides two strands.

It is usually in the petiole of the cotyledon that the transition

¹ In many conifers, where the seed-leaves are numerous and needle-like, a single bundle is sometimes all they possess.

from this ancient even-bundled type to the odd-bundled angiospermous condition of the blade takes place by the fusion of the two central bundles or branches to form a midrib (Fig. 4, *b, c, d, e, f*). This may occur in various ways and at various levels, but the result is always the production of a midribbed cotyledon unlike that characteristic of gymnosperms. The two bundles of which the midrib is composed often do not fuse, but run close together through the blade and diverge again widely near the tip of the cotyledon.

DISCUSSION

It is therefore evident, from a study of only a few of its features, that the structure of the seedling displays various categories of characters differing in the amount of conservatism which they possess. The number of protoxylem groups and the level of transition (together with many other characters) vary from species to species and from genus to genus; the number of main veins in the cotyledon (whether one, producing a pinnate blade, or three, five or more, forming a palmate one), and the method of insertion of the cotyledonary traces, are much more constant and distinguish families or groups of families; the main type of venation of the cotyledon (whether midribbed or dichotomous) is still more constant and serves to distinguish angiosperms from gymnosperms; and finally the type of cotyledonary trace (the double bundle and its modifications) is essentially uniform throughout all seed plants.

No general statement that the seedling as a whole is "conservative" or "variable" can therefore well be made. Certain of its characters are highly conservative and certain others are highly variable, the emphasis placed on the one group or the other having led to the differences of opinion as to the general conservatism of the seedling. Indeed, it should be recognized that throughout the plant body it is not particular organs or regions which are less variable than others, but particular *characters of the plant*. In certain structures, especially the flower, these conservative characters are very noticeable, as in the relations of coalescence, adnation and number. Such a large number of other floral characters are highly variable, however, that it is obviously impossible to regard the flower *as a whole* as conservative. So many conservative characters have recently been found in different parts of the plant as to suggest that when our knowledge of comparative plant anatomy is more complete, we shall find that no

one region possesses a very much larger proportion of these slowly changing features than does any other. Of course we must recognize that a given character may be variable in one family or group and conservative in another. This emphasis on the single character, however, rather than on the whole structure, in a consideration of variability, is clearly in harmony with modern conceptions of heredity.

The very fact that there are such things as "conservative characters," which for some reason have become so firmly fixed in the germ-plasm that they have been consistently less variable than others throughout large groups of organisms during evolutionary history, is, of course, what makes it possible for us to recognize relationship and to construct a "natural system" of classification. A clear demonstration of this principle is one of the chief contributions of phylogeny to those sciences which are concerned with the method of evolution.

SUMMARY

1. The present paper is a comparative study of the structure of the seedling throughout the Dicotyledons, with a view to determining the degree of conservatism which it exhibits.

2. Certain features, notably the number of protoxylem clusters and the level of transition from root to stem structure, were found to be very variable, thus confirming the results of other investigators.

3. Of much more constancy was found to be the relation between the vascular system of the hypocotyl and that of the epicotyl. Two main types were recognized; that in which the cotyledonary trace makes but a single gap in the epicotyledonary system, and that in which more than one gap (usually two, three or four) is produced.

4. The venation of the cotyledon, whether of three main palmate veins or of a single strong midrib with weak side veins, was found to be very constant.

5. An *odd* number of veins in the cotyledon (a midrib, usually with one or more pairs of main lateral veins) was found to characterize the seedling of all dicotyledons, and to distinguish it from that of gymnosperms with broad cotyledons.

6. The most conservative character in the anatomy of the seedling is the structure of the cotyledonary trace, which throughout dicotyledons is a double bundle or a modification of it, a type universal among seed plants and also, at least primitively, in the foliage leaf of ferns and gymnosperms.

7. The seedling of dicotyledons is therefore variable in certain of its characters and conservative in others, thus emphasizing the importance of studying conservatism and variability in connection with particular characters rather than with particular organs or regions.

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CONNECTICUT AGRICULTURAL COLLEGE,
STORRS, CONNECTICUT

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